The influence of live-capture on the risk perceptions of habituated samango monkeys

Katarzyna Nowak[a,b]* ; knowak02@gmail.com

Shane A. Richards[c,d] ; shane.richards@csiro.au

Aliza le Roux[b] ; leroux.aliza@gmail.com

Russell A. Hill[a,e] ; r.a.hill@durham.ac.uk

[a] Evolutionary Anthropology Research Group, Department of Anthropology, Durham University, South Road, Durham DH1 3LE, United Kingdom

[b] Department of Zoology and Entomology, University of the Free State, Qwaqwa, Phuthaditjhaba 9866, South Africa

[c] Department of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, UK

[d] Current address: CSIRO Oceans & Atmosphere, P.O. Box 1538, Hobart, Tasmania 7001, Australia

[e] Primate & Predator Project, Lajuma Research Centre, P.O. Box 522, Makhado 0920, South Africa

* Corresponding Author (Katarzyna Nowak; knowak02@gmail.com; +44 07400482343)

Running Heading: *Measuring effects of live-capture on monkeys*

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Live-capture of animals is a widely used technique in ecological research, and previously trapped individuals often respond to traps with either attraction or avoidance. The effects of trapping on animals' risk perception are not often studied, even though non-lethal effects of risk can significantly influence animals' behavior and distribution. We used a combination of experimental (giving-up densities: GUDs) and behavioral (vigilance rates) measures to gauge monkeys' perceived risk before and after a short live-trapping period aimed at ear-tagging monkeys for individual recognition as part of on-going research. Two groups of arboreal samango monkeys, *Cercopithecus albogularis schwarzi*, showed aversion to capture in the form of generalized, group-level trap shyness after two individuals per group were cage-trapped. We predicted that trapping would increase monkeys' anti-predatory behavior in trap vicinity, and raise their GUDs and vigilance rates. However, live-capture led to no perceptible changes in monkeys' use of space, vigilance or exploitation of experimental food patches. Height above ground and experience with the experiment were the strongest predictors of monkeys' GUDs. By the end of the experiment, monkeys were depleting patches to low levels at ground and tree heights despite the trapping perturbation, while vigilance rates remained constant. The presence of cage traps, re-introduced in the final 10 days of the experiment, likewise had no detectable influence on monkeys' perceived risk. Our findings, consistent for both groups, are relevant for research that uses periodic live-capture to mark individuals subject to long-term study, and more generally to investigations of animals' responses to human interventions.

Keywords: Live-trapping; ear-tagging; giving-up density; vigilance; African guenon

INTRODUCTION

Live-capturing is a necessary technique in many studies of wild mammals where external markings are added to enable observers to distinguish individuals (Glander et al. 1991; Rocha et

al. 2007; Stone et al. 2015), where tracking collars are affixed to study animals' movement patterns (Moehrenschlager et al. 2003), or biological samples are obtained (Fietz 2003). Seldom, however, are the effects of live-capture and associated handling on study animals' behavior explicitly investigated and even where data are available, they suggest inconsistent patterns of responses ranging from avoidance to attraction. For example, adult and juvenile coyotes (*Canis latrans*) become trap-shy after initial captures using box traps (Way et al. 2002). Coyotes that were trapped and released without sedation strictly avoided traps in the future and, once an individual from their social group had been trapped, other group members stayed away from traps (Way et al. 2002). Trap aversion has also been reported during a related study on San Nicolas Island, where the island fox, *Urocyon littoralis dickeyi*, avoided areas in which they had been trapped, altering their ranging behavior in favor of areas where trapping had not occurred (Jolley et al. 2012). In contrast, some species become trap happy and excessive recaptures need to be reduced. For example, recaptures of the endangered fox, *U.l. clementae*, were reduced by using bait treated with odorless salt (Phillips and Winchell 2011).

Other responses to trapping include signs of short-term stress. Live-capture induces a stress response in meadow voles (*Microtus pennsylvanicus*) (Fletcher and Boonstra 2006) and ground squirrels (Delehanty and Boonstra 2009) but has no long-term effect on the stress physiology of mouse lemurs (*Microcebus murinus*), which readily habituate to trapping and are therefore easily re-trapped (Hämäläinen et al. 2014). Rhesus monkey (*Macaca mulatta*) mothers that have experienced an extended period of trapping on Cayo Santiago were more likely to maintain proximity with their infants, and less likely to encourage independence or reject infants (Berman 1989). Recent research on red colobus monkeys (*Procolobus rufomitratus*) shows that they responded similarly to darting and collaring as to a predatory attack by chimpanzees (*Pan troglodytes*) (Wasserman et al. 2013) – with an acute but short-term stress response. This finding is consistent with the "risk-disturbance hypothesis," which stipulates that human disturbance can be similar to, or even exceed natural predation risk (Frid and Dill 2002). In contrast, a study of

the effects of trapping on baboons (*Papio hamadryas*) and vervet monkeys (*Cercopithecus aethiops*) found no obvious effects on individual or group behavior, nor did animals become more wary of traps following previous capture (Brett et al. 1982). The length and frequency of capture, as well as the type of species under study, all appear to influence response type and magnitude.

While animals may quickly learn the association between their captors, the captors' tools (e.g., traps), and danger, it remains unclear if non-lethal human "predators" can influence the perceived risk and therefore foraging costs of wild animals. At the most basic level, we expect wild animals' threat-sensitive responses to be affected by persistent human activities (Frid and Dill 2002). For example, where woolly monkeys (*Lagothrix poeppigii*) are hunted, they learn to distinguish between three types of humans: hunters, gatherers, and researchers, responding most strongly to hunters (Papworth et al. 2013). Other mammals, such as ungulates, may not as readily distinguish hunting from other human activities. Red deer (*Cervus elephus*) respond with increased vigilance to both recreational park users and hunters, although overall vigilance levels are higher in the hunting season (Jayakody et al. 2008). Roe deer (Benhaiem et al. 2008) and mountain gazelle (*Gazella gazelle*) (Manor and Saltz 2003) become more vigilant when and where they are hunted or exposed to "human nuisance behavior". Red deer (*Cervus elaphus*) shift habitats, trading off feeding opportunities to avoid human hunters (Lone et al. 2015) and Nubian ibex (*Capra nubiana*) do the same in response to tourists (Tadesse and Kotler 2012).

The majority of studies investigating this risk-disturbance hypothesis have assessed relatively crude changes in vigilance behavior and range use. To maintain optimal fitness, animals could make smaller-scale behavioral adjustments and discriminate between objects or contexts that vary in risk level. For example, monkeys are known to increase vigilance and decrease foraging time in the lower forest strata (Makin et al. 2012). Our study aimed to investigate short-term and local changes in microhabitat use (including vertical height) and rates of vigilance in reaction to humans and traps. We assessed if a habituated primate will distinguish

between non-threatening human observers, who may actually be perceived as offering protection from natural predators (Nowak et al. 2014) and potentially dangerous traps left by the observers, adjusting their behavior accordingly. We measured the effects of live-trapping, aimed at marking individuals as part of an on-going long-term study, and subsequent placement of cage traps on monkeys' perceived risk and associated foraging cost for two groups of habituated samango monkeys (*Cercopithecus albogularis schwarzi*). We employed two commonly adopted approaches for quantifying risk perceptions: giving-up densities (GUDs) and rates of vigilance. GUDs represent the amount of food a forager gives up in a food patch, with lower GUDs predicted in areas where animals feel safe and have a higher food harvest rate (Brown 1999). In contrast, higher vigilance interferes with feeding (Brown 1999; Benhaiem et al. 2008), and is expected to raise GUDs. We predicted that both indirect measures of risk (GUDs and vigilance rates) would increase relative to the baseline (pre-capture) rates, at least in the short-term (days), following both live captures and the subsequent placement of traps within the experimental area where monkeys forage on artificial feeding stations.

MATERIALS AND METHODS

Study site and subjects.---We conducted our study between May and September 2013 at the Lajuma Research Centre (23°02'23''S, 29°26'05''E) in the western Soutpansberg Mountains, Limpopo Province, South Africa (Nowak et al. 2014). The site is characterized by fragments of tall moist forest (up to 20 m high) and short dry forest (up to 10 m high) (Coleman and Hill 2014a). Monkeys' natural predators include leopards (Chase Grey et al. 2013), crowned (*Stephanoaetus coronatus*) and black (*Aquila verreauxii*) eagles, caracals (*Caracal caracal*), and rock python (*Python sebae*). Sympatric diurnal primates are chacma baboons (*Papio ursinus*) and vervet monkeys (*Chlorocebus aethiops pygerythrus*).

We studied two groups of samango monkeys, which belong to the polytypic *Cercopithecus mitis* group widely distributed across Africa but rare in South Africa, where they

are limited to Afro-montane and coastal forest fragments (Dalton et al. 2015). They are medium-sized (up to 70 cm; 4.4 kg for adult females, 7.6 kg for adult males; Harvey et al. 1987), group-living arboreal monkeys with a mostly frugivorous diet (Coleman and Hill 2014b). Our two study groups consisted of 40 and 60 individuals, respectively. Since the beginning of 2012, both groups – called Barn and House – have been followed by researchers (3-4 times per week) as part of a long-term behavioral study and are thus well-habituated to human presence. Both groups had previously experienced GUDs experiments and cage-trapping, but never in combination or in temporal proximity as in this experiment.

Giving-up densities.---Giving-up densities were measured for 20 days (4 consecutive days per week for 5 weeks) both before and after the pre-baiting (8 days) and live-capture periods (5 days). Artificial foraging patches were established at 16 trees, randomly selected within groups' known winter home ranges, in short forest adjoining tall evergreen forest. At each GUDs patch, we suspended basins at four heights: 0.1, 2.5, 5, and 7.5 meters. Each basin (46 cm in diameter) was filled with 4 liters sawdust and "baited" daily with 25 shelled raw peanut halves. We counted remaining peanuts every day after 1600 h and topped up any spilled sawdust (Nowak et al. 2014). The pre-baiting and live-capture took place within this experimental patch area.

Live-trapping.---The main purpose of the live capture was to ear-tag monkeys for identification purposes in the context of a large on-going scientific research project at this site. We took advantage of these captures to answer our questions about the specificity of monkeys' responses. All trapping procedures were approved by the Limpopo Province Department of Economic Development and Tourism, with ethical approval from Durham University's Life Sciences Ethical Review Process Committee and the Anthropology Department's Ethical Sub-Committee. Our research followed ASM guidelines.

The trapping period was preceded by eight days of pre-baiting, consisting of baiting with orange quarters two custom-made cage traps (123 cm long x 60 cm wide x 80 cm tall) per group. Monkeys (including previously ear-tagged individuals from an earlier trapping event in 2012) took oranges from traps on a regular basis during this period. Active trapping was then initiated and four individuals (all untagged) were trapped and marked, two from each group, on the first two days of the five-day trapping period (Fig. 1). Samango monkeys forage as a cohesive group (Emerson and Brown, 2013) and other group members were moving through the trapping area when individuals were trapped (mean neighbors within 5 m = 1.79 (SD = 1.89) (Coleman 2013), and they dispersed in response to the capture events and/or other individuals dispersing. Trapped individuals were hand-injected with Zoletil within minutes (<5 min) of capture by an experienced veterinarian, and carried to a nearby area to be measured, ear-tagged, and finally placed in a holding cage during recovery. Three of the four captured individuals recovered quickly (one adult female reacted strongly to the anesthetic), and all four were released within a mean of 3.7 (SD = 0.79) hours of capture back into their social group. All animals subsequently were monitored and returned to typical activity patterns the following day. The traps were supplemented with additional bait, consisting of bananas and passion fruits, in the ensuing three days of the trapping period to try and increase the probability of further captures. These same cage traps were later re-placed, open and without bait, next to GUDs trees in the final 10 days of the 20-day post-trapping experimental period.

Vigilance.---Vigilance behavior of monkeys while foraging on artificial food patches was recorded either by observers, standing with binoculars at no less than 20 m from GUDs trees (during monkeys' first foraging bout of the day), or using camera traps (Cuddeback Attack IR and Bushnell Trophy Cam) in the absence of observers (throughout the day). "Vigilance" referred to a monkey looking or glancing up from an experimental basin to visually scan the area in an upright posture. Vigilance data were recorded from the point at which a monkey began

foraging within an experimental food patch and ended when the monkey left the basin (n = 85 records before trapping and 72 after trapping for Barn group; 220 before and 177 after for House group). Vigilance was extracted from camera trap video footage based on the same criteria for the start and end of a bout (n = 16 video clips before and 20 after capture for Barn group: 30 before and 108 after for House group) for a total of 728 records. The number of glance-ups per minute constituted "vigilance rate". For statistical purposes, data from direct observations and camera traps were pooled following assessment that there were no statistical differences between these two data sources.

Analyses.---As prior research detected subtle effects of human followers on monkeys' perceived risk of predation (Nowak et al. 2014), we analyzed only data from days on which monkeys were not followed from dawn to dusk by researchers. To appropriately account for the structured nature of data collection (i.e., repeated sampling at trees), and the fact that the data were highly over-dispersed, we developed likelihood functions that incorporated these effects. This more general approach also allowed us to better link our biological hypotheses with our study design (Richards 2015). Specifically, we fitted discontinuous temporal models of GUDs and vigilance rates to our data to investigate whether or not our two experimental disturbances (live-capture and the presence of cages post-trapping) resulted in short-term changes in foraging behavior, while still allowing for any underlying gradual changes in foraging behavior. For both the GUD and the vigilance data sets we fitted models that incorporated up to three predictive factors: the sampling day of the GUDs experiment (D: 1-40), the period of the study delineated by the two imposed disturbances (P: pre-trap [days 1-20], post-trap without trap stimulus [days 21-30], and post-trap with trap stimulus [days 31-40]), and the height of the food basin (H: ground and aboveground, which included the three tree-level basins). Thus, D reflects long-term responses (weeks), P reflects short-term responses (days) in the form of break-points, and H reflects local responses (meters). Random variation in foraging behavior among basins, caused by unknown

differences among the trees sampled, and day-day site-wide differences (e.g. variation in weather), were also explicitly incorporated into the models. In brief, our GUD model is a generalized example of a logistic regression, and our vigilance model is a generalized example of a non-linear regression, where P and H are treated as discrete factors, D is a covariate, and day-day variation is a random effect. Also, for both models, we account for additional sources of over-dispersion in the data. Full details of the statistical models can be found in Supporting Information S1. Evidence that any of the three factors improved model parsimony and explanatory power was evaluated by performing model selection using AIC (Richards 2015).

RESULTS

During the first phase of our study (sampling days 1-20), before animals were introduced to the traps, we observed samango monkeys foraging within all of our basins. During the pre-baiting phase, when traps were placed at two trees within both groups' foraging range but not set to trigger (eight consecutive days), animals continued to forage at basins placed on trees associated with the trap, and also removed bait from the cage traps (Fig. 1). After traps were set to trigger (trapping phase) only two animals per group were caught and catches occurred only on the first two days of the trapping period (Fig. 1). No trapping location was successful on more than a single day. Animals in both groups continued to feed near the areas where the captures took place but individuals avoided approaching or entering the set traps despite the presence of significantly enhanced bait in each of the traps.

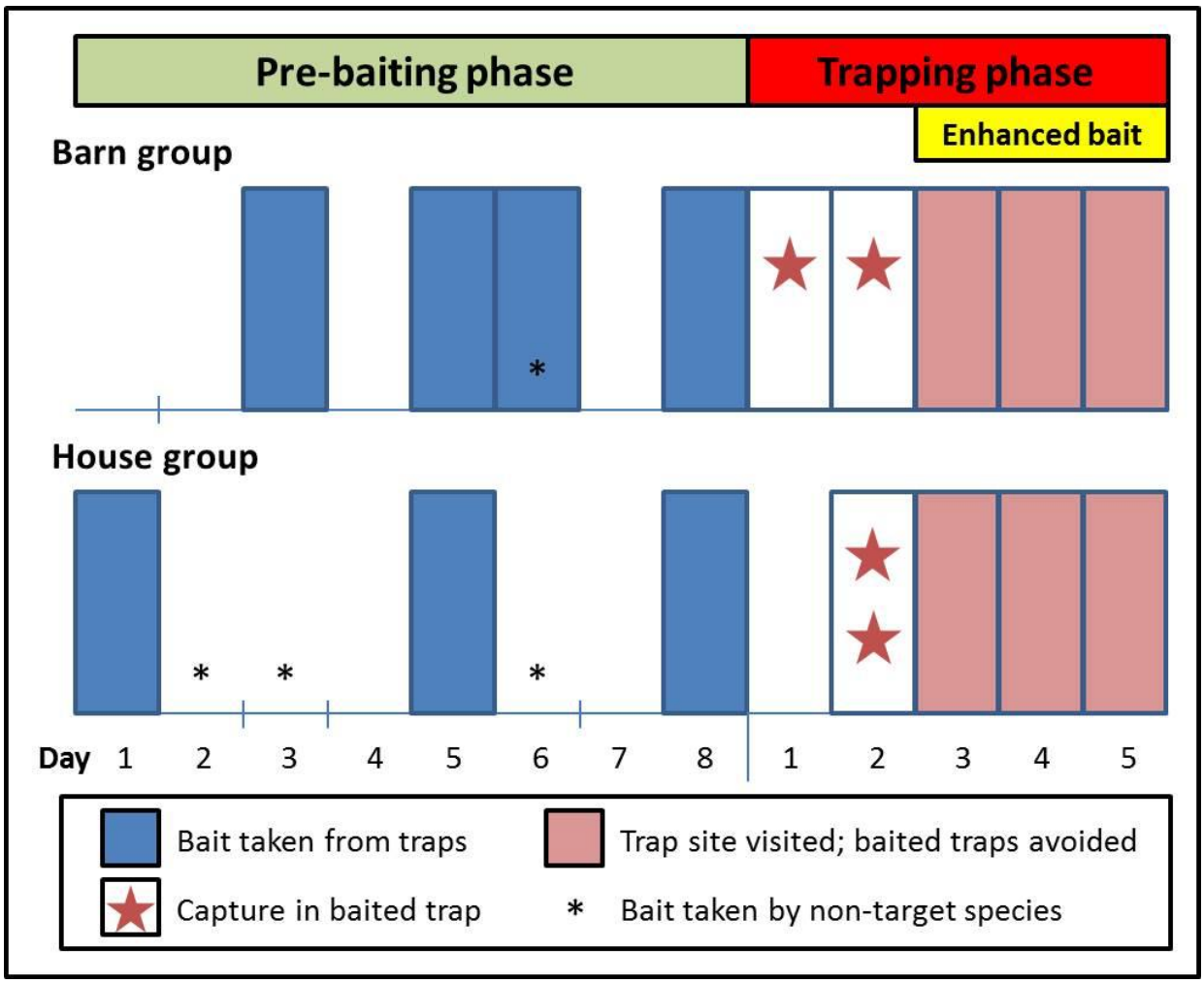

Fig. 1. Samango monkey (*C. albogularis schwarzi*) responses to traps placed near feeding stations during the pre-baiting and trapping phase of the study, carried out from May to September 2013 in the Western Soutpansberg Mountains, South Africa. Each day, from 6th-18th July 2013, a trap was placed at two trees within the foraging range of House and Barn groups. Traps always contained food but they were not set to trigger during the pre-baiting phase. Bars depict days that samango monkeys were observed at one or more traps; blue bars indicate that samango monkeys removed bait from traps, whereas red bars indicate that bait within traps was avoided. On four days during pre-baiting baboons or vervet monkeys removed food from the traps before samango monkeys arrived (asterix). Four samango monkeys were caught during the trapping phase (red stars): two adult females (AF), one in each group, a juvenile female (JF) in House group, and a sub-adult male (SM) in Barn group.

GUDs (measured as number of peanuts remaining in basins) declined gradually over the course of the study and GUDs were lower for basins placed aboveground for both groups (Fig. 2a,b). However, there was no obvious short-term change in GUDs after live-capture for either group (sampling days 21-40). Re-placing traps back in the foraging area (days 31-40) did not raise monkeys' perceived risk as measured by GUDs and rates of vigilance. These conclusions are supported by our AIC analyses selecting the model including height and day (H+D) as the best

model for both groups (Table 1). While the model including sampling period and height (P+H) also was considered parsimonious for Barn group (Table 1), temporal changes in GUDs could be better explained by assuming a gradual decline over time rather than a response to trapping. We found no evidence of a gradual change in the rate of vigilance for either group, nor did we find any evidence of a short-term vigilance response to trapping (Fig. 2c,d). However, both groups significantly elevated vigilance behavior when foraging on the ground (only model H was selected for both groups: Table 1) and, in general, House group (the larger of the two study groups) was less vigilant.

Table 1. Summary of the AIC analyses of the GUD and vigilance data for two groups of samango monkeys (*C. albogularis schwarzi*) studied in the Western Soutpansberg Mountains, South Africa from May to September 2013. Models incorporated up to three factors for both data sets: day of sampling (D), period of sampling (P), and patch height (H). *K* is the number of estimated model parameters, LL is the maximum log-likelihood, and ΔAIC is the difference in the AIC of the model compared to the lowest AIC model. Bold ΔAIC values indicate that the model is selected (i.e., is relatively more parsimonious, given the models considered). Models were selected if they had ΔAIC < 6 and no simpler, nested model had a lower AIC score (Richards 2015).

	GUD			Vigilance		
Model	***K***	**LL**	**ΔAIC**	***K***	**LL**	**ΔAIC**
Barn group						
Null	10	-1945.1	33.7	10	-152.4	16.2
D	11	-1940.0	25.6	11	-152.3	18.0
P	12	-1938.9	25.2	11	-152.0	17.5
D+P	13	-1938.9	27.2	13	-151.7	20.9
H	11	-1933.9	13.3	11	-143.3	**0.0**
H+D	13	-1925.2	**0.0**	12	-142.9	1.3
H+P	15	-1924.0	**1.4**	15	-140.7	2.9
H+D+P	17	-1923.6	4.7	16	-140.7	4.9
House group						
Null	10	-1528.9	35.2	10	-285.9	51.4
D	11	-1519.1	17.6	11	-285.8	53.2
P	12	-1520.7	22.8	11	-285.1	51.8
D+P	13	-1518.6	20.6	13	-284.6	54.9
H	11	-1522.1	23.6	11	-259.2	**0.0**
H+D	13	-1508.3	**0.0**	12	-259.1	1.8
H+P	15	-1511.0	9.3	15	-255.6	0.8
H+D+P	17	-1507.7	6.7	16	-255.2	1.9

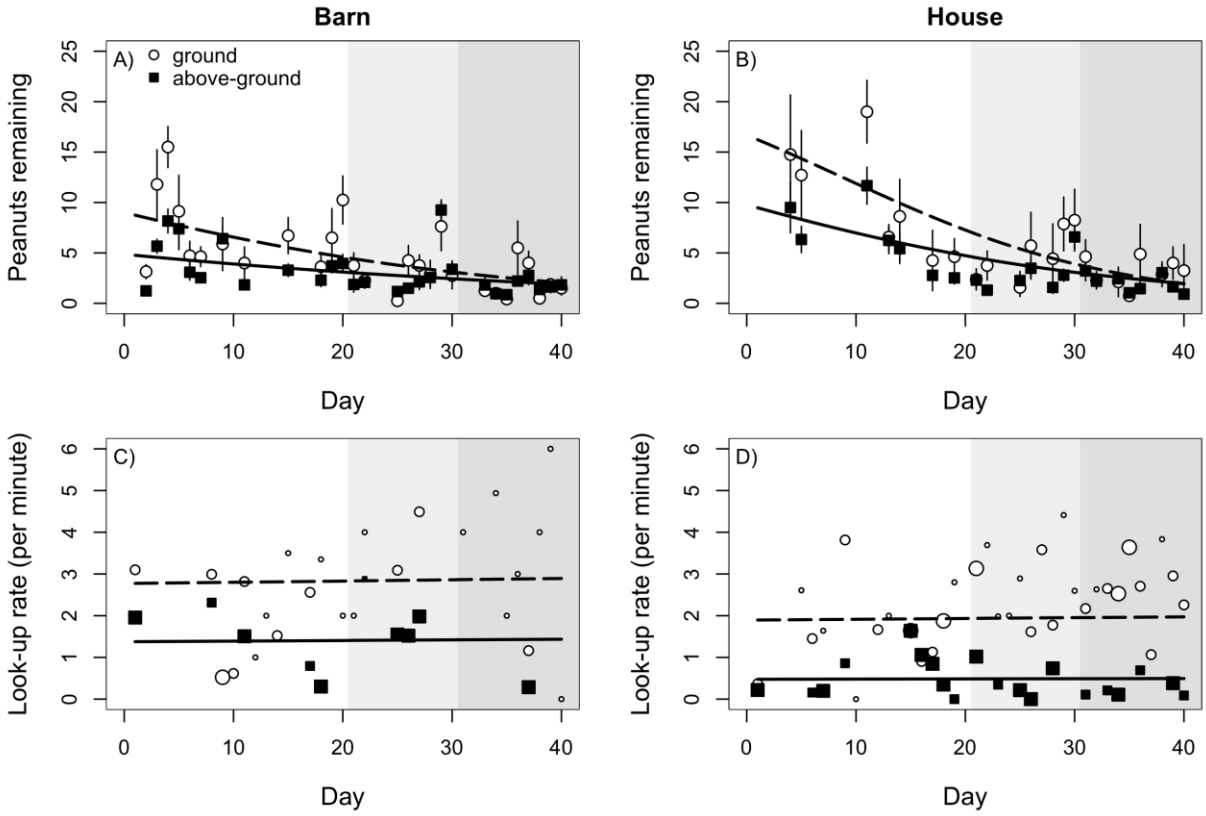

Fig. 2. Observed and predicted GUDs and vigilance rates for two groups of samango monkeys, *C. albogularis schwarzi*, studied in 2013 in South Africa. Time is sectioned into three periods: pre-trap (days 1-20, white), post-trap without trap stimulus (days 21-30, light grey), and post-trap with trap stimulus (days 31-40, grey). Panels A and B show observed GUDs averaged across eight trees for two height categories, and error bars represent 1 se. Sloped lines indicate the best AIC model predictions, which was model D (sampling day) + H (ground or tree) for both groups. Panels C and D show the corresponding vigilance rates. Symbols size indicates the period of the observations used to calculate the mean rate: < 5 minutes (small), 5-15 minutes (medium), and > 15 minutes (large). Again, lines indicate the AIC-best model predictions, which was model H for both groups.

DISCUSSION

We found no evidence for live trapping affecting the anti-predatory behavior (i.e., GUDs and vigilance rates) of these habituated samango monkeys, with the exception of observing the monkeys' trap avoidance following initial successful captures. Their trap shy response may represent long-term individual aversion to trapping and the trap stimulus in that no individual samangos have ever been re-captured at Lajuma (of 18 caught and tagged), while at Hogsback in the Eastern Cape, only 4 out of 64 samango monkeys were re-caught following successful

286 capture (Kirsten Wimberger, University of Cape Town, personal communication, May 2014).
287 This is in contrast to mouse lemurs (Hämäläinen et al. 2014) and galagos (Charles-Dominique
288 and Bearder 1979) which show no aversion to traps or being trapped and therefore re-enter traps
289 on successive occasions.

290 Despite samango monkeys' apparent trap aversion, we nevertheless found no further
291 evidence that live-capture or subsequent placement of traps in the GUDs experimental area
292 altered these samango monkeys' perceived risk, even in the short-term (neither in the days
293 immediately following trapping nor during the five weeks following trapping). Monkeys' typical
294 anti-predator behavior (e.g. vigilance, use of the ground stratum) remained unaltered after the
295 capture events, even while the trap stimulus was present in the experimental area. Monkeys did
296 not transfer their negative trap-response (trap shyness) to our experiment, i.e. the experimental
297 area or the artificial food sources (man-made containers/basins used in the experiment). This
298 suggests that monkeys likely distinguish between anthropogenic sources of risk, possibly
299 because they already had five weeks prior (positive and rewarding) experience with experimental
300 food patches before the live-capture. The food patches (raw unshelled peanuts) were also of high
301 quality and required no processing once found inside the sawdust.

302 Where samango monkeys face a variety of risks including conflict with people and
303 depredation by domestic dogs, such as in Hogsback, Eastern Cape, South Africa, they will still
304 capitalize on high-quality food in the form of fallen exotic oak acorns and seeds in people's
305 gardens (Wimberger et al. in review). Supplementing the cage traps in this study with additional
306 high-quality bait (bananas and passion fruits) in the final three days of the live capture, however,
307 failed to attract the trap-averse monkeys.

308 Despite the absence of evidence suggesting behavioral changes in space-use and
309 vigilance in response to capture, animals did exhibit consistent, predictable variation in risk
310 responses in relation to foraging height and experience with the GUDs experiment. Monkeys had
311 higher GUDs at the start of the experiment, foraged less at ground level (Emerson et al. 2011;

Nowak et al. 2014) and had lower vigilance rates at higher canopy levels (MacIntosh and Sicotte 2009; Campos and Fedigan 2014). The larger House group had lower vigilances rates than the smaller Barn group, consistent with the group size effect (Hill and Cowlishaw 2002; Makin et al. 2012; Campos and Fedigan 2014). Animals also showed a steady increase in foraging proficiency over the course of the experiment, suggesting that practice and familiarity may result in falling GUDs; GUDs decreased over time at ground and tree levels, indicating monkeys' ability to quickly adapt to their current environment and efficiently exploit newly available sources of food from which they were not easily deterred by a perturbation like live-capture.

We found no evidence of a trade-off between vigilance rates and GUDs; GUDs declined but vigilance rates were fixed throughout the duration of the study. However, we have only quantified vigilance rates and not duration of vigilance; it may be that look-up duration declined over time, which freed up time for lowering GUDs. We had enough video data of House group foraging to see if time spent at trees changed during the study, and, if it differed between basin heights. We found no evidence of a day effect on the mean time spent at trees (ANCOVA; $F_{1,31}$ = 2.67, P = 0.112); however, there was evidence of a height effect (ANCOVA; $F_{1,31}$ = 9.40, P = 0.004) with monkeys spending less time at ground than tree canopy level (Supporting Information S2). On average, over the course of the day, animals spent shorter times at the basins placed on the ground (3.26 ± 0.75 minutes) compared with basins placed aboveground (8.56 ± 1.67 minutes). These additional findings suggest that animals improved their proficiency at finding peanuts rather than spending more time at basins, given that the amount of peanuts taken from basins increased over time but time spent at basins did not increase.

While we did not measure hormones or stress responses directly like Wasserman et al. (2013), we similarly did not find monkeys' behavior to be suggestive of a prolonged stress response as a result of the live-capture. The monkeys in our study appeared to be extremely apt at distinguishing among different forms of risk and clearly made trade-offs that optimized their

exploitation of food-rich patches (Emerson and Brown 2013). While the monkeys, like coyotes and foxes (Way et al. 2002; Jolley et al. 2012), became trap shy, their trap aversion did not result in or extend to spatial avoidance of the area in which trapping took place as it did for the carnivores. This has important implications in management terms, as the use of trapping and release would not be a worthwhile approach to deterring primates from food sources. Our research indicates that primates are unlikely to show a generalized fear response following live-capture, particularly if carried out by humans to whom they are already habituated.

Where goals are to study primates long-term by habituating them, insights about the risk-disturbance hypothesis, specifically fear, risk avoidance and learned responses to humans and their research tools, are important for conservation managers looking to monitor endangered species. The methods we used here are generalizable to other longitudinal field studies that employ live capture to mark and study animals. Further comparative data are essential to gauge the relative differences among species and individuals in responses to capture and other potentially stressful research practices, such as wearing of GPS collars. This study is important for understanding how our research and management practices may distort animal behavior – or even cause harm – and result in misinterpretation of wild animals' resilience to our presence and activities.

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SUPPORTING INFORMATION

Supporting Information S1. Full details of statistical models and analysis of giving-up densities and vigilance.

Likelihood function describing GUDs.---Giving-up densities (GUDs) and vigilance behaviors were recorded for two groups of samango monkeys: Barn and House. The two groups foraged at separate but nearby sites. At each site four basins were placed on 8 randomly selected trees. One basin, termed the ground basin, was placed at the base of the tree (10 cm above the ground) and the remaining three basins, termed aboveground basins, were placed at 2.5 m, 5 m and 7.5 m. At the start of the day 25 peanuts were placed in each basin mixed in with sawdust and at the end of the day the number of peanuts remaining (GUD) was recorded. GUDs were recorded during three time periods: pre-trap (sample days 1-20), post-trap without a trap stimulus (sample days 21-30), and post-trap with a trap stimulus (sample days 31-40). Additional details of the experimental protocol can be found in Materials and methods.

We assumed that the mean fraction of peanuts remaining in basins at the end of the day could be described by the following piecewise logistic function:

$$\text{logit}\,\bar{y}(t) = \begin{cases} \beta_0 + \alpha(t-1), & \text{if } 1 \le t \le 20; \\ \beta_1 + \alpha(t-21) & \text{if } 21 \le t \le 30; \\ \beta_2 + \alpha(t-31) & \text{if } 31 \le t \le 40; \end{cases} \quad \text{(S1)}$$

where

$$\beta_1 = \beta_0 + 20\alpha + \delta_1 \quad \text{(S2)}$$

and

$$\beta_2 = \beta_2 + 10\alpha + \delta_2. \quad \text{(S2)}$$

β_0 describes the degree to which peanuts are depleted on sample day t = 1, α describes how GUDs change gradually over sampling days, and δ_1 and δ_2 describe rapid changes in GUDs due to the trapping event and the reintroduction of a trap stimulus, respectively.

To describe the patterns of GUDs in our data we needed to explicitly account for three sources of random variation. Random day-day variation in the fraction of peanuts remaining in basins on individual trees (within-tree variation) was accounted for by incorporating the beta-binomial distribution with variance parameter ϕ (Richards 2008). Between-tree variation in GUDs was accounted for by associating each tree with a parameter u, which were estimated from the data; trees having a lower u tended to have more peanuts removed. Random day-day variation in GUDs across trees caused by site-wide factors (e.g., weather conditions) were incorporated by assuming that sampling days were associated with a random variate, Z, drawn from a normal distribution with mean zero and standard deviation, σ_z; days associated with a low z-value resulted in all trees at the site experiencing fewer than the expected number of peanuts.

Let y_{ijt} be the number of peanuts remaining in basin j located on tree i on sample day t. The assumptions described above define our model, which is described by the set of parameters, $\boldsymbol{\theta}$. The probability of observing all the data at a site, denoted $\mathbf{Y}$, given our model, is:

$$\Pr(\mathbf{Y} \mid \boldsymbol{\theta}) = \prod_{t=1}^{40} \int_{z=-\infty}^{\infty} f_{\mathrm{N}}(z \mid 0, \sigma_z) \prod_{i=1}^{8} \prod_{j=1}^{4} f_{\mathrm{BB}}(y_{ijt} \mid 25, T[\bar{y}_j(t), u_i + z], \phi)\, dz \quad \text{(S4)}$$

where

$$T[p,w] = \frac{e^w p}{1 - p + e^w p}, \quad \text{(S5)}$$

f_N is the probability density function of the normal distribution, and f_{BB} is the probability mass function of the beta-binomial distribution with variance parameter ϕ (see Richards 2008 for details). Here we have added a subscript *j* to the population expectation $\bar{y}(t)$ as we allow for the associated parameters to vary depending on whether or not the basin is place on the ground. We equated this probability of the data with the likelihood of the model and estimated the log-likelihood using

$$\mathrm{LL}(\boldsymbol{\theta} \mid \mathbf{Y}) = \sum_{t=1}^{40} \ln \sum_{k=-K}^{K} \exp\left[\ln f_k + \sum_{i=i}^{8} \sum_{j=1}^{4} \ln f_{\mathrm{BB}}(y_{ijt} \mid 25, T[\bar{y}_j(t), u_i + \sigma_z z], \phi) \right] \quad \text{(S6)}$$

where $2K+1$ is the number of intervals used to approximate the standard normal distribution, $z_k = 8k/(2K)$, and

$$f_k = \frac{e^{-z_k^2/2}}{\sum_{m=-K}^{K} e^{-z_m^2/2}}. \quad \text{(S7)}$$

We found $K = 20$ gave an accurate estimate of LL.

Likelihood function describing vigilance.---The rate of looks performed per minute for both groups was modelled in a very similar manner as the GUDs; however, the within-tree variation in the number of looks was assumed to have a negative-binomial distribution with variance parameter ϕ (see Richards 2008 for details), rather than a beta-binomial distribution. As the number of looks is unbounded we modified the expected number of looks by replacing the logit transformation on the left side of equation (S1) with the natural logarithm, ln. Also, because we had less temporal resolution for the look data (Fig. 1) we forced α to be equal for both the ground and aboveground basins.

Model selection.---Eight models were considered for both groups when investigating both the GUD and the vigilance data (Table 1). Models included zero or more of the following three effects: (D) sampling day, (P) sampling period, and (H) basin height. Factors were removed from a model as follows: (D) $\alpha = 0$, (P) $\delta_1 = \delta_2 = 0$, (H) β_0, α, δ_1 and δ_2 were set equal for both heights. For all models we assumed random within-tree variation ($\phi > 0$), between-tree variation ($u_i \neq 0$), and day-day variation ($\sigma_z > 0$). Models were selected using the recommendations of Richards (2015); namely, all models with ΔAIC within 6 of the minimum are initially selected, but complex models with simpler, nested models having a lower AIC score, were subsequently discarded.

Supporting Information S2. ANCOVA analysis of basin visit times.

ANCOVA analysis of basin visit times.---Vigilance behaviors were examined using both direct observations and reviews of video. The video data provided a standardized approach for measuring the time spent at basins during the day. Between one and two trees were videoed at a site on any given day. 90% of visits to basins occurred between 6:00am and 9:30am. Unfortunately, we only had enough video data to statistically analyze House group. Foraging times for House group did not appear to change over time, however animals appeared to spend less time at the ground basins (figure S1). These patterns were investigated using an ANOVA, in which we log-transformed the times to normalize residuals, treated sampling day as a covariate, and treated basin height as a factor with two levels: ground, aboveground. The statistical analysis was performed using the lm function in R v. 3.1.3 (www.r-project.org).

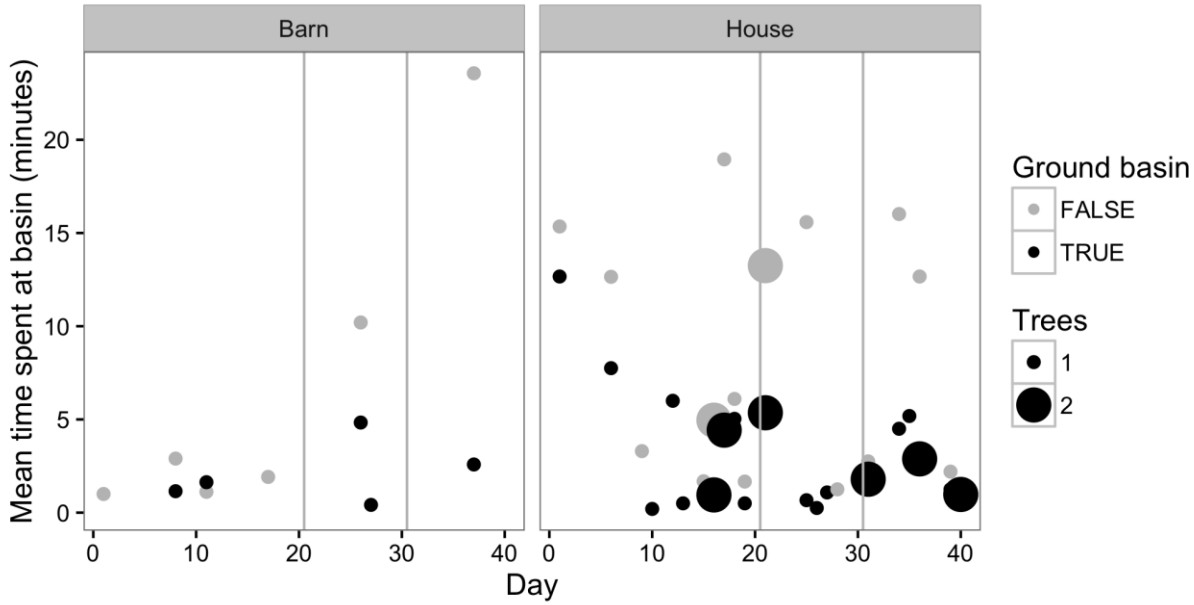

Figure S1. Mean time each day that experimental basins with peanuts established in the home ranges of two monkey groups were visited during our study in Western Soutpansberg Mountains, South Africa in 2013. Video data are presented for the two groups of monkeys we studied, and basins have been grouped according to whether or not they were placed on the ground, the most risky stratum for arboreal monkeys. The number of trees videoed each day is also indicated. Vertical blue bars delineate the two experimental manipulations that delineate the three periods: pre-trapping, post-trapping without trap stimulus, and post-trapping with trap stimulus.

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